males from one experiment produced the following progeny when crossed with wild type:

| | Wild type | B1 | D | B1D | Total |
|---|---|---|---|---|---|
| A | 361 | 0 | 0 | 361 | 722 |
| B | 424 | 0 | 0 | 390 | 814 |

It is obvious that there was complete linkage between B1 and D, indicative of a translocation between chromosomes 2 and 3. If the original X-rayed males had been mated to normal XX females, and the male offspring selected for testing, interchanges between Y and any of the other three chromosomes could have been detected.

Cytological examination at meiosis was difficult because of the extremely small nuclei. Observations of the somatic chromosomes at metaphase in nerve ganglia (Dobzhansky 1931), and in ovarian tissue (Painter and Muller 1929) were easier because of their greater length. The frequent tendency for parallel orientation of the homologues reflected the new positions of the end segments in the interchange heterozygotes. With the discovery of the usefulness of the salivary gland chromosomes, it was possible to locate the cross-shaped configurations with reference to the banding patterns and thus determine precisely the breakage positions. This is difficult or impossible when the breaks are in heterochromatic regions, since these regions are represented by few or no bands in the banding pattern.

Interchanges may be detected by examining the chromosomes at metaphase in somatic tissue and comparing their morphology with that of normal individuals. It is being used on white blood cells and various other cells in man.

Methods using genetic markers also serve to identify the linkage groups and the chromosomes involved in the interchange.

## Methods of identifying the chromosomes involved in interchanges

The chromosomes involved in the interchanges in maize were identified by various means. Some of the methods used or that could be used are listed and described below. Not all can be used for every species; the ones to be used depend on the previous cytogenetic information on the species, the stocks available, and the behavior of interchanges in that species. The possible methods are:

Method 1. Test for linkage between partial sterility and marker genes as described earlier (page 70). In self-pollinating crops such as barley, $F_2$ and $F_3$ data are relatively easy to use to determine recombination values. Formulas for the calculation have been derived (Hanson and Kramer 1950).

Method 2. In the interchange heterozygote, test for linkage between markers in different linkage groups, as described in the previous section.

Method 3. Identification of the chromosomes involved in the cross-shaped pachytene configuration in the interchange heterozygote, as described on page 67. This method is usable only if the chromosomes stain and spread well enough to permit recognition of the cross-shaped configuration. Identifications of the chromosomes that have exchanged segments are easier if the centromeres can be identified, if there are knobs or other distinctive markers, and if the relative arm lengths and the positions of these distinctive

markers in the normal chromosomes are known. If the position of the center of the cross is variable, the procedure has been to use the average of the various "cross" positions unless differences in chromomere density or in other markers permit an accurate placement of the break positions.

This method has not been successful in barley because of the difficulty in getting satisfactory pachytene preparations, although a preliminary pachytene map has been published (Sarvella et al. 1958).

Method 4. In somatic tissue, e.g. root tips in plants, nerve ganglia or white blood or other cells in mammals, compare chromosome lengths and arm lengths in heterozygous and homozygous interchanges with those in normal plants. The same may be done for the interchange homozygote at pachytene. It has been used successfully for several of the interchanges in barley by Hagberg and Tjio (1950, 1952) and Hagberg (as reported by Burnham and Hagberg 1956). It serves to identify the chromosomes involved in the interchange only if the pieces exchanged are considerably different in length, or if one of the breaks occurs in a distinctive region, as e.g. in a satellite.

In Drosophila, in interchanges involving the small, dot-like chromosome 4, the new length of 4 indicates the relative length of the segment received by 4 (Dobzhansky 1930).

Method 5. Examine cytologically at meiosis the trisomic $F_1$'s from identified primary trisomics crossed as ♀ with the interchange. In the trisomic $F_1$ plants a ring of four plus a separate trivalent ( ⊙ 4 + III) indicates the extra chromosome is not one of those involved in the interchange, while a chain of five indicates that it is. This was used in the identification of semisterile-3 in maize (Burnham 1948). If the tester stock is trisomic for a chromosome that has been identified cytologically, the test is very useful; and even more so if in addition, as in maize, the linkage group has been identified with the chromosome. Unless the trisomics show high transmission or are phenotypically recognizable, the method is not very efficient. The 2n + isochromosome and 2n + telocentric stocks might be useful also.

Method 6. Examine cytologically at meiosis the $F_1$ of crosses between interchange stocks. This method is relatively free of errors and may be used for those species which are not analyzable by pachytene observations. The crosses between semisteriles-1, -2 and -3 described on page 68 are examples of its use. If the $F_1$ has 2 ⊙ 4, the two chromosomes involved in one interchange complex are different from those in the other. If the $F_1$ has a ⊙ 6, one chromosome is involved in both interchanges. An $F_1$ between interchanges involving the same chromosomes will not show an association of more than four chromosomes, it may show only or mostly "pairs".

A tester set of interchanges may be selected which will identify the chromosomes involved in any unknown ⊙ 4. Ones giving frequent "chains" or "pairs" when heterozygous are not satisfactory as testers. In maize, observations at mid-diakinesis are the most reliable, but in barley observations at metaphase I are the easiest to use. The first interchanges found in a species may be intercrossed, and letters may be assigned arbitrarily to the interchanged chromosomes based on the cytological configurations in $F_1$. This procedure was used in barley (n=7), and a set of five testers was established: a-b, b-d, c-e, e-f and c-d. The first four will identify all but four (e-f, e-g, a-d and b-g) of the 21 possible combinations. When this set is used, the g chromosome is identified by elimination (Burnham et al. 1954). For the fifth tester, any one of 11 combinations would serve (Ramage, personal communication) but a b-g or e-g would furnish a positive test for g and also identify the four not identified by the remainder of the set. The chromosomes of barley were subsequently described cytologically and numbered 1 to 7 based

mainly on length (Hagberg and Tjio 1950). The linkage group carried by each was determined later and also the correspondence between the temporary letters and the numbers; i.e. 1 = b, 2 = f, 3 = c, 4 = e, 5 = a, 6 = g and 7 = d (Kramer et al. 1954, Burnham and Hagberg 1956, Ramage et al. 1961). Hence the first tester set used is 1-5b, 1-7a, 3-4a, 2-4a and 3-7a. If a 1-6a interchange is used in place of 3-7a, none of the seven chromosomes has to be identified by elimination.

In maize, the set of six testers that has been used is sufficient to identify all ordinary interchanges between two chromosomes includes interchanges T1-2a, T2-4d, T3-7c, T5-7c, T8-9a, and T8-10b. Since almost invariably chromosome 6 is attached to the nucleolus, its presence in an unknown ring can be determined by the association of the ring with the nucleolus at diakinesis. The tester set in barley and in corn may be used to determine the linkage groups as well as the chromosomes involved in new interchanges; since the chromosome numbers correspond to those of the linkage groups.

A general scheme is helpful in selecting a set of testers. For a hypothetical group of three chromosomes designated a, b, c; the following three sets of two are equally usable in identifying the presence of a, b or c in an unknown ring: (1) a-b and b-c, (2) a-b and a-c or (3) a-c and b-c.

Any one of the three possible sets may be used. In corn, if the satellited chromosome 6 is omitted, there are nine chromosomes left to be identified by the tester set, i.e. three groups of three, for each of which two testers are needed or a total of six. Using this scheme it is easy to select complete sets of six from the available interchanges whose chromosomes have been identified.

It may be of interest to determine the number of different sets of six that are possible for the nine chromosomes designated from a to i. The number of interchanges involving a in sets of three, i.e. a with two others, is $8c_2 = \frac{8'}{6'\ 2'} = \frac{7.8}{1.2} = 28$. For each set of three, there are ten different ways of selecting the other two sets of three. For any one set of three chromosomes, there are three ways of selecting the two testers needed, or 3x3x3 = 27 combinations of six testers for each group of nine chromosomes. The total number of possible different complete sets of six testers is: 28 x 10 x 27 = 7,560.

## Origin and occurrence of interchanges

*Natural occurrence*

At least 15 naturally occurring cases of semi-sterility due to chromosomal interchange in genetic stocks and in breeding material have been established in corn (Brink 1927, Emerson (Unpub.), Burnham 1930, Stadler 1931, Clark 1942, Anderson 1935). Occasional partially sterile plants have been found in the garden pea, barley, rye, rice and in many other species, (for a summary, see Burnham, 1956).

The original exchange may have come about from breakage and reunion as interlocked bivalents separate at the first division of meiosis (Sax and Anderson 1933); from the spontaneous association of heterochromatic regions (Kostoff 1938), by crossing over between duplicated segments in non-homologous chromosomes (Müntzing 1934), or presumably from breakage resulting from natural radiation. In Oenothera hookeri (7II), interlocking bivalents were observed in 50% of the nuclei (Wisniewska 1935).

Interchanges have been detected in the progeny of plants homozygous for the "sticky" chromosome character in corn (Beadle 1937), in the progeny of plants carrying the Acti-

vator and Dissociation mutation-controlling elements (McClintock 1950, 1951); and also in plants grown from aged seed in wheat and in barley (Gunthardt et al. 1953).

INTERCHANGES IN GEOGRAPHIC RACES. In maize a survey of geographic races has shown that interchanges have become established only rarely. Cooper and Brink (1937) reported one in a strain from Manchuria, p. 103, while Rhoades and Dempsey (1953) reported no interchanges or inversions in the exotic strains they tested.

On the other hand, a survey of 583 collections of Datura made by Blakeslee et al. (1937) showed that homozygous interchanges have become established in local populations of this species (Table 28). Prime type 1 was the standard with which all were crossed.

**Table 28.** Distribution of chromosomal prime types among 583 races of Datura stramonium (Blakeslee et al., 1937, from Table 3, p. 1078, Cytologia, Fujii Jub. Vol.).

| Origin | No. of localities tested | Total races | No. of races of each prime type 1 | 2 | 3 | 4 | 7 | 87 | 88 | Prime types occurring together |
|---|---|---|---|---|---|---|---|---|---|---|
| Canada | 1 | 1 | 1 | | | | | | | |
| U.S.A. | 155 | 216 | 162 | 24 | | 32 | 15 | | | 2+7,4+7,2+4,2+4+7 |
| West Indies | 11 | 16 | 6 | 5 | | 4 | 5 | | | 2+7,4+7 |
| Central America | 7 | 10 | | 10 | 3 | | | 1 | | 2+3,2+87 |
| So. America | 58 | 81 | 15 | 61 | 51 | | | | 1 | 2+3 |
| Europe | 82 | 140 | 8 | 125 | 1 | 23 | 8 | | | 2+3,2+4,2+7,4+7,2+4+7 |
| Asia | 23 | 33 | 7 | 26 | | | | | | |
| Africa | 18 | 26 | 3 | 12 | | 12 | 12 | | | 2+4,4+7,2+7 |
| Australia | 5 | 5 | 1 | 2 | | 2 | 2 | | | 4+7 |
| Hawaii | 2 | 4 | | | | 1 | 4 | | | 4+7 |
| Bot. Gardens, or Commercial | | 51 | 14 | 29 | | 6 | 8 | | | 2+4,4+7 |
| Totals | 362 | 583 | 217 | 294 | 55 | 80 | 54 | | | |

As shown in Table 28, the type selected as the standard, called prime type I (PT1), was the most common one in the U.S.A. It is the one whose chromosome ends are designated 1.2, 3.4, 5.6, 7.8 etc. to 23.24. Six other prime types were found, two of them, 87 and 88, only once. The end arrangements in the translocated chromosomes in the different interchanges were as follows:

| | | | |
|---|---|---|---|
| PT2 | 1.18 | 2.17 | |
| 3 | 11.21 | 12.22 | |
| 4 | 3.21 | 4.22 | |
| 7 | 9.20 | 19.10 | |
| 87 | 3.12 | 4.22 | 11.21 |
| 88 | 15.23 | 16.24 | |

Five of these differ from PT1 by one interchange, but chromosome 21.22 is involved in a different interchange in PT3 and PT4. PT87 which differs from PT1 by two interchanges might have originated by a later interchange in PT3 or PT4. PT1 was not found in Central America. PT2 was the predominant race in Central and South America, Asia and in Europe, and was the type found in standard races of several other species. Hence it may have been the more primitive type. Since PT3 was always associated with PT2, it probably originated in PT2. Since crosses between different PT2 geographic races gave

no indication that they differed, they concluded that they represented one occurrence that subsequently spread. It would be of interest to know if the different PT3's, 4's etc. were the same also. Since changes in end arrangements have become established in Datura, they are of potential importance in evolution. They concluded that the relatively small number of prime types in wild populations made it unlikely that new phenotypes with duplications would arise in nature from intercrosses between interchanges involving the same chromosomes or from the other types of crosses by which they experimentally produced true-breeding lines with extra chromosome material (page 106).

*Induced interchanges*

Interchanges have been induced in maize by X-ray irradiation of pollen (Stadler 1930, 1931), or seed (Anderson 1935, 1936); by exposure of seed at the Bikini and Eniwetok bomb tests (Longley 1950, 1959); and by exposure of pollen or seed to thermal neutrons (Schmidt and Frolik 1951). Similar treatments have produced interchanges in barley, rice, cotton and several other species. The rate is dependent on dose, but may be 10 to 20% or even higher with thermal neutrons which are less damaging than X-rays.

When seed of maize was X-rayed the changes occurred in sectors, often three to five or more qualitatively different changes were observed in the same tassel (Anderson et al. 1949, Randolph 1950, p. 113). Occasional plants from treated seed in barley have shown an association of many chromosomes as a result of multiple exchanges (Caldecott and Smith 1952). These large rings were not usually transmissible to their progeny. If they involved homologues as well as non-homologues, meiosis could not produce haploid gametes with a complete set of chromatin.

In maize, when seed was produced from pollinations with X-rayed pollen, the resulting plants were either normal, or the entire plant carried the change in heterozygous condition, there were no sectors. Sectors might be expected if the chromosomes in the sperm were double at the time of irradiation. However, even if double, breakage in both might have occurred.

When the partially-sterile plants among the progeny from irradiated pollen were progeny-tested in the next generation, only part of them transmitted the partial sterility. A pollen grain with a normal tube nucleus but a deficient sperm should be functional. This will account for those plants that were partially sterile but had only normal progeny. In general, only very small deficiencies survive the gametophyte screen in higher plants.

In Drosophila, changes induced in the sperm have been studied in crosses made with irradiated males or irradiated impregnated females. Some of the changes produced act as dominant lethals, as indicated by reduced egg hatch.

Treatment of pollen with ultra-violet light, a non-ionizing radiation, has produced chromosomal interchanges in tomatoes (Barton 1954). In maize, only deficiences were produced, about 80% of which were fractional, i.e. only part of the tissue of the zygote carried the deficiency (Stadler 1931). Singleton and Clark (1940) reported breakages and transpositions in maize, but not interchanges. Pachytene

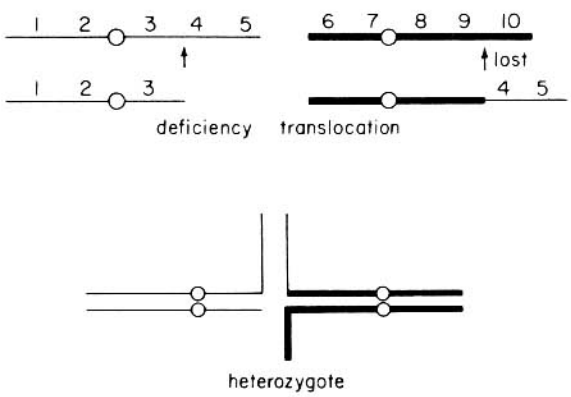


FIG. 25. Diagrams showing the probable constitution of a deficiency translocation resulting from the loss of one segment (this writer's interpretation of the description by Singleton and Clark, 1940). The 2-chromosome combination of donor and recipient chromosomes is inviable.

configurations were often T-shaped or supposedly of the type shown in Fig. 25.

From such a figure, no viable 2-chromosome combination carrying either or both of the changed chromosomes is possible.

Certain chemicals have been found to produce chromosome breakage, e.g. phenols, coumarin, sodium citrate, aluminum chloride, urethanes (see Oehlkers and Linnert 1951), and nitrogen and sulfur mustards and mustard gas (see Auerbach 1951). In most of these studies tests of transmission to their progeny were not reported. Interchanges have been produced by treatment of Drosophila males with nitrogen mustard (Kaufmann et al. 1949). The rate was highest in males mated 13-18 days after treatment (3.09% in one experiment, 2.29% in another). The rate was about 50% higher when pre-treated with near infra-red. The break positions showed essentially a random distribution among the limbs of chromosomes 2 and 3, and the Y and 4 chromosomes.

## Break positions and frequencies

Breaks have occurred in all the various kinds of distinctive markers in the maize chromosomes, i.e. in the satellite as in T1-6b (Burnham 1932a, T3-6 Clarke and Anderson 1935), nucleolar organizer as in T6-9b (McClintock 1934), in a centromere (McClintock 1931), and at various other positions in the chromosomes. The pieces exchanged may be short, medium or long, or any combination. One or both may include only one or two chromomeres, but only if these are distinctive in size or shape can the nature of the change be determined, as in those with breaks in the satellite mentioned above.

Large numbers of interchanges in maize produced from seeds exposed to X-rays, to radiations at the Bikini and Eniwetok bomb tests, at Oak Ridge, and some from X-rayed pollen have been established and made available largely by the work of Anderson and Longley. The chromosomes involved and the break positions have been reported (Longley 1950, 1958, 1961). The 1961 publication lists the breakage positions of all the interchanges for each chromosome in order from the distal end of the short to the distal end of the long arm, making it relatively easy to determine if one with break positions at the points desired for a given experiment has been found. For critical work the break positions should be rechecked, since the positions listed may have a sizable error. Some may be checked as homozygotes. For those with breaks in the distal portion of the short arm of 6, this would identify those with breaks in the nucleolus organizer or in the satellite. Interchanges between all the chromosomes are available.

The number of breaks observed in each chromosome in the 1002 interchanges that have been analyzed at pachytene in corn are summarized in Table 29.

**Table 29.** Summary of observed interchange break frequencies for 1002 interchanges in maize and numbers expected if frequencies are proportional to length at pachytene.

| | Chromosome | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Total |
| % of total length | 14.9 | 12.0 | 11.2 | 10.6 | 10.8 | 8.8 | 8.5 | 8.6 | 7.8 | 6.7 | 552.66 u* |
| Obs. breaks | 249 | 217 | 204 | 199 | 263 | 189 | 160 | 206 | 186 | 131 | 2004 |
| Calc. no. | 299 | 241 | 225 | 213 | 217 | 177 | 170 | 172 | 157 | 134 | |
| o/c | .833 | .900 | .907 | .934 | 1.212 | 1.068 | .941 | 1.198 | 1.185 | .978 | |

* Longley, 1939.

The numbers of breaks were roughly proportional to length, but with a definite tendency for the longer chromosomes to have fewer breaks than expected and the short ones more than expected (except for chomosome 10, the shortest one).

The frequencies of exchanges between long arms, short arms, and long and short arms, based on 591 interchanges in Longley's 1958 report, are shown in Table 30.

**Table 30.** Interchange frequencies between arms that are long, medium or short (l, m, s).

| | l-l | l-m | l-s | m-s | m-m | s-s | total no. |
|---|---|---|---|---|---|---|---|
| Obs. no. | 164 | 187 | 119 | 69 | 37 | 16 | 591 |
| Calc. no. | 186.8 | 173.6 | 117.2 | 54.6 | 40.4 | 18.4 | |

The 1-1 combinations were fewer than expected, 1-m and m-s greater than expected. Calculations using these same interchanges indicate no strong tendency for pieces of equal length to be interchanged (Burnham and Yagyu, unpublished).

The observed frequencies of break positions in 5u intervals from the centromere compared with those calculated if at random are shown in Table 31.

**Table 31.** Translocation break frequency in maize in relation to distance from the centromere, as tabulated by Longley (1950).

| Dist. from cent. | Obs. | Cal. | o-c | o/c | o/c* |
|---|---|---|---|---|---|
| 0-5u | 302 | 213 | + 89 | 1.42 | |
| 5-10 | 333 | 213 | +120 | 1.56 | 1.432 |
| 10-15 | 149 | 182 | - 33 | 0.82 | |
| 15-20 | 132 | 160 | - 28 | 0.83 | 0.841 |
| 20-25 | 107 | 145 | - 38 | 0.74 | |
| 25-30 | 101 | 121 | - 20 | 0.83 | 0.752 |
| 30-35 | 39 | 89 | - 50 | 0.44 | |
| 35-40 | 10 ) | | | | 0.422 |
| | ) | 54 | - 41 | 0.24 | |
| 40-45 | 3 ) | | | | 0.403 |
| Total breaks | 1176 | | | | 2004 |

* Based on 2,004 breaks (Longley 1961)

The data in Table 31 show that breakage was more frequent than expected in segments up to 10u from the centromere; and less frequent than expected from that point to the end, the greatest deficiency being in the distal segments of the longer arms.

In the 1961 report, the o/c value for the frequency of breaks in the long arm of chromosome 7 was 1.60, 0.32, 1.16 and 0.33 in successive intervals of 10u from the centromere. The second peak was in the region of the subterminal knob, in agreement with Longley's conclusion that the breakage frequency was higher in the heavily-staining regions. Also, as the dosage increased, the number of breaks in those regions increased and the number in the lightly-staining regions decreased.

Information is needed in maize on the accuracy with which the average position of the center of the "cross" indicates the true breakage points for interchanges, and to determine if there may be a tendency for the "cross" to shift predominantly in one direction when breaks are in certain regions. Even if true, it is not likely to account for so great a discrepancy as that observed.

In Datura, based on 169 translocations from treatment and 13 naturally-occurring ones, there is no evident relationship between frequency and chromosome length (Blakeslee et al. 1937).

In Drosophila the frequencies of translocations resulting from several X-ray experiments are summarized in Table 32.

**Table 32.** Frequencies of translocation breaks in Drosophila chromosomes from X-ray treatment of males in experiments using genetic markers.

| Reference | Chromosomes tested* | Fertile ♂ tested | Sex Chrom. | No. of breaks II | III | IV | No. of transloc. |
|---|---|---|---|---|---|---|---|
| Muller & Altenburg 1930 | X, 2, 3 | 282 | 7 | 22 | 21 | | 25 |
| " | Y, 2, 3 | 110 | 3 | 13 | 16 | | 16 |
| " | Y, 2, 3, 4 | 420 | 8 | 57 | 53 | 6 | 62** |
| Dobzhansky 1930 | X, 2, 3, 4 | 121 | | 4 | 9 | 5 | 9 |
| " | sex, 2, 4 | 426 | 10 | 14 | | 4 | 14 |

* Chromosomes between which interchanges could be recognized.

** One male was heterozygous for a Y-3 and a 2-4 translocation.

The data in Table 32 suggest that chromosome 4 had a far greater number of breaks than expected based on its relative length, the sex chromosomes usually fewer than expected. As expected, the frequencies in 2 and 3 were about equal.

Later studies showed the break frequency to be proportional to the mitotic rather than the salivary length, and that eu- and heterochromatic regions were about equally breakable. For example, Kaufmann (1939, 1946) found that 23% and 25% of the breaks in X were in the proximal heterochromatin. Correction for undetected exchanges within the heterochromatin which includes 1/3 of the mitotic length brings these values up to 28% and 30% respectively (Lea 1947). The distribution of 475 breaks along the remainder of the chromosome was fairly uniform (Kaufmann 1939). In the later report, the distribution of 1048 breaks among divisions 1 to 19 (20 is the heterochromatic region) showed a "slight but general increase in break frequency in the distal portion." Also there were wide deviations from expected frequencies in certain intercalary subdivisions, too great to be due entirely to chance. One possible explanation is the presence of intercalary heterochromatic regions that are physically longer than indicated in the salivary gland chromosome. Two-break frequencies within the X-chromosome (inversions) were 2 1/2 times as frequent as expected, whereas translocations between the X and 2 and 3 were considerably lower, as shown in Table 33.

There was an indication of a significant increase of observed over expected numbers of inversions in the X that include 12 or 13, 25 or 26, and 42 or 43 subdivisions. This suggests a coiling pattern that may increase the opportunities for inversion of parts sepa-

**Table 33.** Frequencies of X-chromosome inversions and of translocations between X and chromosomes 2 and 3 (Kaufmann 1946).

| | Inversions in X | | Translocations | |
|---|---|---|---|---|
| | Obs. | Expected | Obs. | Expected |
| 2-break exchanges regions 1 to 19 in X | 87 | 34.22 | 305 | 357.78 |
| 2-break exchanges one break in 20 | 53 | 24.90 | 142 | 170.10 |

rated by one or more turns of the coil (Kaufmann 1946). There was no tendency for new breaks to be clustered around the points of inversion in the delta-49 inversion stock used for part of the treatments. In a later report, treatment of the inversion heterozygote produced breaks at or near the original points of breakage. The distribution of breaks among the four limbs of chromosomes 2 and 3 from X-ray treatment as reported by Bauer et al. (1938) and Bauer (1939) and from nitrogen mustard treatments (Kaufmann et al. 1949) was essentially at random. At the higher dosage of X-rays (4,000r), the more complicated types of exchanges were more frequent than expected, as analyzed by Lea (1947).

Treatment of the female germ cells in Drosophila produced a much lower frequency of translocations (Glass 1956). At an average of about 2,000r, the frequency was about 6% in the progeny of treated males and only about 0.06% (one case) in those from treated females. Two possible reasons were offered: (1) the mature ♀ germ cells had not passed through meiosis (they were still diploid), (2) the chromosomes were farther apart and moved less.

## Viability of interchange homozygotes

If interchanges are the result of mere exchanges of segments, one might expect the homozygotes to be viable. In Drosophila, less than half of them are fully viable. The others are lethal or lower than normal in viability or in fertility (Table 34).

**Table 34.** Viabilities of males and females heterozygous or homozygous for the same translocation in Drosophila (tabulated from Bridges and Brehme 1944).

| | Homozygotes for translocations involving | | | Heterozygotes for translocations involving | | |
|---|---|---|---|---|---|---|
| | X chrom. | Other chrom. | Total | X chrom. (males) | Other chrom. | Total |
| Number fully viable | 7 | 24 | 31 | 9 | 53 | 62 |
| " lethal | 6 | 21 | 27 | 5 | 0 | 5 |
| " semilethal or viable but sterile | 6 | 8 | 14 | 15 | 0 | 15 |
| Totals | 19 | 53 | 72 | 29 | 53 | 82 |

Table 34 shows that male flies heterozygous for translocations involving the X also frequently have lower than normal viability, but heterozygotes for translocations involving the other chromosomes are fully viable. A probable explanation of this difference in viability in heterozygotes is the presence of a small deficiency or a recessive lethal